CHEAP TRANSPORT FOR FISHING SPIDERS (ARANEAE, PISAURIDAE): THE PHYSICS OF SAILING ON THE WATER SURFACE

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ABSTRACT. Many pisaurid spiders inhabit the edges of bodies of fresh water and actively propel themselves across the water surface using both rowing and galloping gaits. They also sail across the water, taking advantage of the wind and their nearly frictionless interaction with the water surface. The physical interactions of *Dolomedes triton* (Walckenaer 1837) (Araneae, Pisauridae) with moving air, in a wind tunnel in which the floor was water, formed the core of the present investigation. Spiders in an elevated (sailing) posture were subjected to greater drag forces attributable to air motion than were spiders in a prone (non-sailing) posture and therefore were transported substantially faster than prone spiders. In the context of transport velocity, the benefit of adopting an elevated posture was substantially greater (relative to mass) for small spiders than for large ones, although even under the relatively steady flow conditions of the wind tunnel the velocities of the small spiders in the elevated posture were more variable than either small prone spiders or large spiders. The efficacy of adopting an elevated posture was a consequence of the steep air velocity gradient that existed above the surface of the water in the wind tunnel and that also exists above any pond over which the air is moving. Taken as a whole, the data indicate that sailing is a remarkably cheap form of transportation for *Dolomedes*, but that, at least at the edges of large bodies of water, it involves risks because it is directionally uncontrolled.

Locomotion by spiders includes ordinary terrestrial modes such as walking, running, and jumping, and quite unusual modes of airborne and aquatic locomotion. Although the eight-legged stepping patterns of spiders on land obviously differ in detail from those of insects (Cocatre-Zilgien & Delcomyn 1993), the biomechanics of terrestrial locomotion by insects and by spiders probably differ little because they share size (Price 1984; Pennycuick 1992), exoskeletal architecture, and important aspects of the nervous system (Osorio et al. 1995, 1997). Consequently, the rich literature on the biomechanics of terrestrial locomotion in insects (e.g., Full & Tu 1990; Full et al. 1995) contributes substantially to our understanding of terrestrial locomotion in spiders. The same cannot be said of the biomechanics of aerial dispersal via ballooning and of locomotion on the water surface, forms of spider locomotion that are shared by only a few insects (ballooning: McManus & Mason 1983; Cox & Potter 1986; aquatic locomotion: Andersen 1976). For these unusual modes of locomotion, most of our knowledge of the physics and biomechanics comes from the literature on arachnids (ballooning: Humphrey 1987; Suter 1991, 1992; aquatic locomotion: Suter et al. 1997; Suter 1999a).

Fishing spiders, *Dolomedes triton* (Walckenaer 1837) (Pisauridae), the subjects of this paper, actively propel themselves across the water surface using two distinct gaits: rowing propels the spiders horizontally at velocities < 0.27 m/sec (McAlister 1959; Shultz 1987; Suter et al. 1997) and galloping, used by these spiders during some kinds of prey-capture (Gorb & Barth 1994) and during escape from predators (Suter unpubl. data), propels the spiders at horizontal velocities up to 0.75 m/sec (Suter 1999a). In both rowing and galloping, the spider accelerates forward by rapidly moving its propulsive legs backwards, transferring momentum to the water through the generation of drag. These active aquatic gaits are distinct from the alternating tetrapod locomotion used by the spiders on solid substrate (Barnes & Barth 1991; Shultz 1987).

Fishing spiders also move across the water surface propelled by air movements. Deshefy (1981) reported on one distinctive form of this "sailing" in which the spider extends and el-

evates its most anterior pair of legs, taking advantage of the increased wind speed 2–3 cm above the water surface. I have observed a second distinctive form of sailing in pisaurid spiders, in which the spider extends and depresses all of its legs, thereby raising its body well above the water surface and allowing the body and proximal leg segments to interact with more rapidly moving air currents. What follows are analyses of (1) the wind velocity gradient in the boundary layer above a pond's surface, (2) the drag forces acting on elevated vs. prone spiders, and (3) the velocity changes that result from modification of posture during sailing.

METHODS

Pond measurements.—I used a hot-wire anemometer (Thermonetics Corporation model HWA-103) to measure wind speed just above the surface of a pond at The Rockefeller University Field Research Center, Millbrook, Dutchess County, New York. At the time and location of the data collection, the water surface was upwind of the pond's usual shore but was separated from the shore by about 4 m of mud flat. I arranged the anemometer assembly (below) so that its sensor pointed upwind (away from the shore) and was over the water 0.5 m from the edge of the mud flat. As a result of the location and orientation of the sensor, it measured the speed of air that had traveled at least 120 m across the pond's surface unimpeded by structures other than the surface of the water itself. The height of the sensor above the water surface was controlled by a motorized cam which, as it rotated, raised and lowered the 0.5 m boom to which the sensor was attached. The resulting motion of the sensor tip was vertical (in space) and sinusoidal (in time), with a period of 4.3 sec, an excursion from 0.5 to 8.9 cm, and a maximum velocity of 0.06 m/sec (a small fraction of the recorded air velocities).

Analog signals from the anemometer were digitized at 10 Hz by an analog-to-digital (A/D) converter (Vernier Software Co., model ULI 5.0) under the control of data logging software (Vernier Software Co., Logger 3.04) running on a laptop computer (Apple Corporation, model PowerBook 5300c). Power for the computer was supplied by its inboard battery and power for the motorized cam and A/D converter was supplied by a 12 V lead-acid battery.

The analysis of air speed as a function of distance to the water surface was complicated by the high variability in wind speed, presumably due to turbulence, at any single height. Although the mainstream velocity (*sensu* Denny 1993) was unknown for the data collected at the pond, the air's velocity in the boundary layer above the water must decrease to zero as height approaches zero (Denny 1993). Accordingly, I used logarithmic curve fits to characterize the relationship between height and velocity both for the pond data and for the wind tunnel data (below).

Spiders.—The adult *Dolomedes triton* (Araneae, Pisauridae) used in these experiments were collected from small ponds in Mississippi, and the juvenile was the progeny of one of the field-caught females. All were held in my laboratory under conditions described elsewhere (Suter et al. 1997).

In the experiments described below, I investigated the motion of, and the forces acting upon, killed and dried spiders of two sizes. A third-instar juvenile that had been in the lab since hatching (wet mass 0.013 g, 0.126 mN) and two adult males of approximately the same size (0.186 g, 1.82 mN; 0.243 g, 2.38 mN) were anaesthetized with CO_2 and killed by freezing. After post-mortem thawing, the spiders were immobilized in a prone posture (the juvenile and one adult) or an elevated posture (the second adult) and allowed to air dry for several weeks. During the weeks of experimentation, the postures of the adult spiders (Fig. 1) remained unchanged. During measurements of horizontal velocity, however, the posture of the juvenile was changed from prone to elevated to make possible direct comparisons of the same spider in two postures: to accomplish the posture change, I softened the spider's most proximal leg joints by moistening them, and then repositioned the limbs and air dried the spider for several days.

The weights of the dried adult spiders (elevated, 0.736 mN; prone, 0.959 mN) were matched more closely by fastening with epoxy a small, flat coil of nichrome wire (0.221 mN) to the dorsal surface of the cephalothorax of the spider in the elevated posture. The adult spiders then both had weights of 0.96 mN. Temporary weight modifications were accomplished by hanging the same short length of
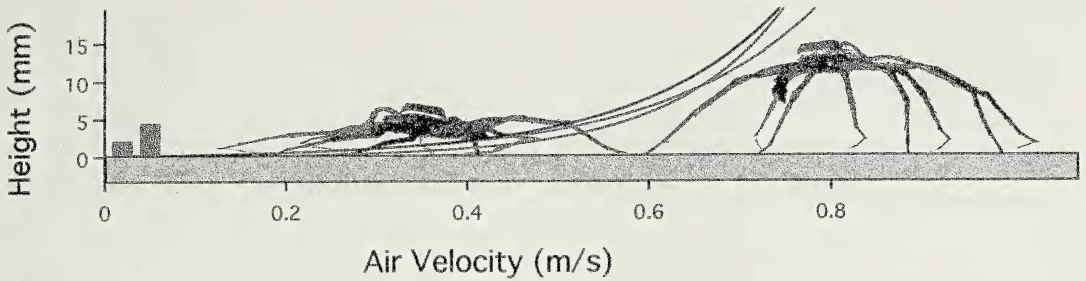
Figure 1.—Adult spider postures as digitized from photographs of the large dried spiders used in the experiments reported here. For comparison, the small spider in the prone and elevated postures had heights of 2.1 mm and 4.4 mm respectively (filled bars at left). A spider in the prone posture (left) is exposed to lower horizontal air velocities than is a spider in the elevated posture (right). The three curves are the same as those shown in Figure 5, but with the axes reversed.

30-gauge copper wire over the cephalothorax of each of the adult spiders. All experiments with the dried spiders were conducted at laboratory temperatures between 20–23 °C.

Wind tunnel measurements.—The horizontal wind tunnel used in this study had an experimental chamber measuring 20 × 20 × 87 cm (length). The floor of the chamber had a 0.6 cm deep cavity beginning 36 cm downwind from the air inlet and having horizontal dimensions of 18 × 40 cm. When the cavity was filled with water, the surface of the water and the surface of the remainder of the floor of the experimental chamber formed an unbroken, flat surface. Both ends of the experimental chamber were fitted with 2 cm thick furnace filter fiber to suppress turbulence. With the exception of the filter, the upwind end of the tunnel was open to room air. Ten cm beyond the filter at the downwind end of the tunnel the air entered a 10.1 cm (diameter) polyvinyl chloride (PVC) pipe on the end of which was mounted a small fan oriented so that it pulled air through the tunnel. Although valving in the pipe leading to the fan allowed me to control air speed in the experimental chamber, I conducted all tests at a nominal air speed of 0.65 m/sec (measured at the center of the air stream, 52 cm from the upwind end of the experimental chamber).

I used a hot-wire anemometer (Thermonetics Corporation, model HWA-103) to monitor air velocity in the chamber and to measure the airspeed profile as a function of the distance from the water surface. The 5 mm (diameter) anemometer probe was inserted through a 6 mm (diameter) hole in the top of the experimental chamber, 52 cm from its upwind end.

A micromanipulator, mounted on the outside of the chamber, facilitated adjustment of the position of the anemometer's sensor relative to the water surface.

At the beginning of a sailing trial, a dried spider was placed gently on the water surface approximately 42 cm from the upwind end of the chamber (6 cm from the upwind edge of the water surface) and at the side-to-side center of the water surface. The spider was held at that location by a pair of nichrome wires assembled in an inverted "V" and attached to a probe that could be raised several cm, releasing the spider. The spider was released only after the tunnel fan was turned on and the chamber had reached a constant nominal velocity of 0.65 m/sec. To measure the sailing velocity of a dried spider, I recorded its location in the horizontal plane, beginning when the spider crossed a line 2.5 cm downwind from its release site, using an SVHS video camera (Panasonic model AG-455) and Image (National Institutes of Health software, version 1.55 f) as a frame grabber and image digitizer (at a rate of 20 frames per second). I digitized the location of the center of the spider's cephalothorax using tools resident in Image, and then calculated velocity as the distance moved divided by the frame interval.

I used a horizontal balance (Suter et al. 1997) to measure horizontal drag forces on the adult dried spiders in the wind tunnel. The balance employed an electronic clinometer (Applied Geomechanics Inc. model 900 Biaxial Clinometer) with a resolution of 0.01° (1.75×10^{-4} rad) to measure small angular displacements that were directly proportional to the horizontal force applied to the spider.
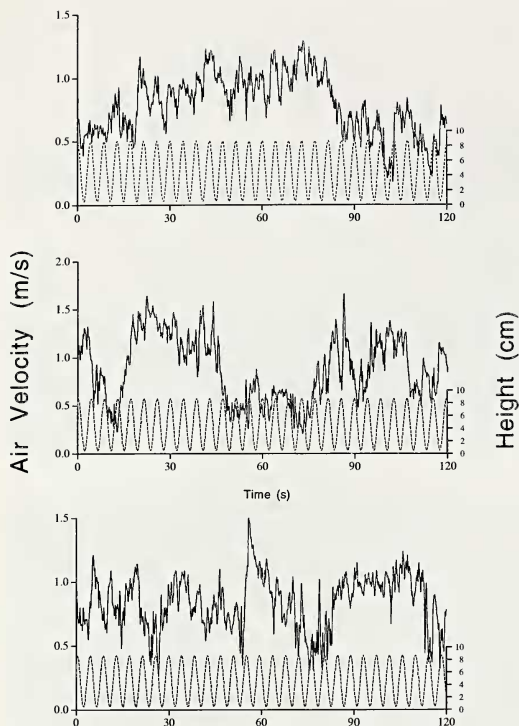
Figure 2.—The horizontal wind speed (solid line) within the 10 cm deep layer of air just above the surface of a pond varied significantly with height of the sensor (dashed line) in each case although the effect was small ($0.04 < r^2 < 0.12$, $P < 0.05$). The residual variability is assumed to be a consequence of the turbulence in the air.

The end of the vertical arm of the balance consisted of a pair of nichrome wires assembled in an inverted "V" which immobilized the spiders without applying any vertical force to them. Clinometer output (in volts) was digitized by an A/D converter (National Instruments Corporation, model NB-MIO-16L) driven by a LabView 3 program (National Instruments) on an Apple microcomputer (Power Macintosh 7100/80AV).

RESULTS

Pond and wind tunnel air movement.— Velocity measurements of the air within 10 cm of the surface of the pond (V_p) indicated that the air was turbulent, with large fluctuations in velocity at several scales (Fig. 2). Only a small amount of the variability in V_p could be attributed to the changes in the position of the anemometer's sensor ($0.04 < r^2 < 0.12$), although the small effect of the
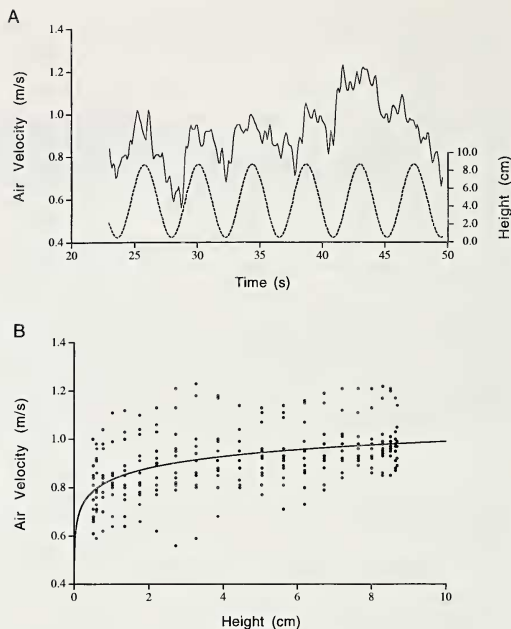

Figure 3.—During a period of relatively constant average wind velocity (23 sec to 50 sec in top graph of Figure 2), velocity of the air just above the pond's surface (A, V_p) varied approximately as the $\log_{10}$ of height (B, assuming, as is required by boundary layer physics, that V_p at the surface must be zero; $V_p = 0.16 \log_{10}$ height $+ 0.83$, $r^2 = 0.225$, $n = 267$, $P = 0.0001$).

height of the sensor was significant ($P < 0.05$ in each sample in Fig. 2). For a subsample of velocity data in which large-scale fluctuations in V_p were relatively small, the influence of sensor height was more prominent and V_p varied approximately as the $\log_{10}$ of height (Fig. 3). The logarithmic relationship between V_p and height can be seen most clearly during short segments of the pond data (Fig. 2) which include only a half cycle or a full cycle of the sensor and therefore do not conflate velocities that are widely separated in time (Fig. 4), and is entirely in accord with boundary layer theory (Schlichting 1979).

In the wind tunnel, constant fan velocity and suppression of some of the turbulence made the influence of height on wind tunnel velocity (V_w) much more detectable: logarithmic curve fits on three data sets indicated that sensor height explained more than 90% of the variation in V_p (Fig. 5; $0.91 < r^2 < 0.97$).

Sailing velocity and drag forces in the wind tunnel.—Images of dried spiders sailing downwind in the wind tunnel indicated that,
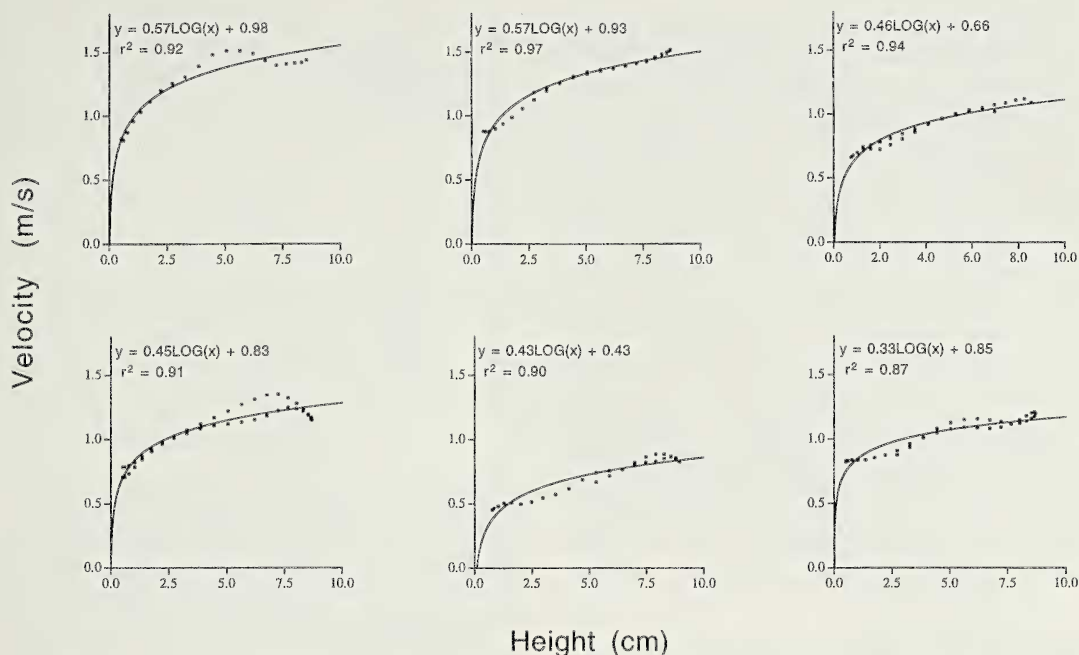
Figure 4.—The relationship between V_p and height above the water is most clearly visible during the brief periods of time (from Fig. 2) which include $\leq$ one full cycle of the sensor and therefore do not conflate velocities that are widely separated in time. In the examples shown here, $\log_{10}$ curve fits worked well: $0.86 < r^2 < 0.98$.

by the time each had reached the line where video digitizing began, it was moving at relatively constant velocity: thus it had reached the terminal velocity (V_t) at which the forces propelling it (air-induced drag) were in balance with the forces resisting its motion (water-induced drag). Under wind tunnel conditions, a large spider (0.42 g, wet weight) dried in an elevated posture always had greater velocities (V_t) than a similar-sized spider that had been dried in a prone posture. At the weights at which the effect of the two postures could be compared directly, being elevated conferred about a two-fold velocity advantage over being prone, but a much greater (3.7-fold) advantage accrued to the elevated form of the very small spider (0.013 g, wet weight) (Fig. 6). A stepwise multiple regression of velocity on height (a function of posture) and weight for the large spider yielded a highly significant relationship ($P < 0.01$, $F = 106.96$, adjusted $r^2 = 0.876$) in which velocity varied directly with height and inversely with weight. For the small spider, the difference between V_t for elevated and prone postures was highly significant (Mann-Whitney U test, $Z =$

-2.646, $P = 0.008$) and the variability in V_t for the elevated small spider was much greater than that for any other group (Fig. 6). The very high variability in V_t for the elevated small spider is probably attributable to small eddies in the air stream close to the water surface that can influence very small objects but are averaged out when interacting with the much greater leg span of the larger spiders.

To test for effects of horizontal orientation relative to the direction of air movement in the wind tunnel, I released dried large spiders at different horizontal orientations, with the expectation that any relationship would be approximately sinusoidal. The orientation of the large dried spiders did not have a significant influence on V_t for either the elevated or the prone spiders (Fig. 7).

In direct measurements of the drag force exerted on spiders by moving air, drag on a spider in the elevated posture was significantly higher than drag on the prone spider (0.055 $\pm$ 0.002 mN $vs.$ 0.029 $\pm$ 0.002 mN; $t = 31.4$, $P < 0.0001$) as expected from the results of dynamic tests (Fig. 6). The 1.92-fold difference between the mean values fits well with
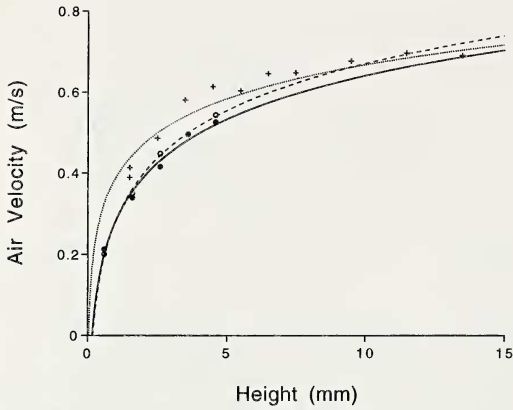
Figure 5.—In the wind tunnel, air velocity (V_w) varied with the $\log_{10}$ of height above the surface of the water. For the three runs shown here, the equations were $V_w = 0.36 \log_{10}$ height $+ 0.28$, $r^2 = 0.987$, $V_w = 0.39 \log_{10}$ height $+ 0.28$, $r^2 > 0.99$, and $V_w = 0.28 \log_{10}$ height $+ 0.39$, $r^2 = 0.920$.

the 2.12-fold differences between measurements of V_t for the identical elevated and prone spiders at their lightest weight (Fig. 6).

DISCUSSION

A fishing spider, lying prone on the surface of a pond and not anchored to floating vegetation or debris, will move passively across the water at a rate influenced by the spider's mass and the velocity of wind over the pond (Fig. 6). The actual air velocity to which the spider is exposed, however, is strongly influenced by the location of the spider's body parts relative to the water surface (Figs. 4, 5). This connection between elevation and air velocity means that the velocity at which the spider can travel under the influence of air movements is closely tied to the spider's posture (Figs. 1, 6).

Quasi-passive locomotion, like ballooning.—Although the propulsive forces involved in sailing are environmental rather than physiological, the importance of posture and the stereotyped performance of the postures employed in sailing (above and Deshefy 1981) indicate that this form of locomotion is not purely passive. On the other hand, because wind direction is not controlled by the spider and because the keel-less spider apparently has no control of its own direction relative to the wind (as do humans in sailboats), the sailing spider cannot influence its destination. In that regard, this quasi-passive form of loco-
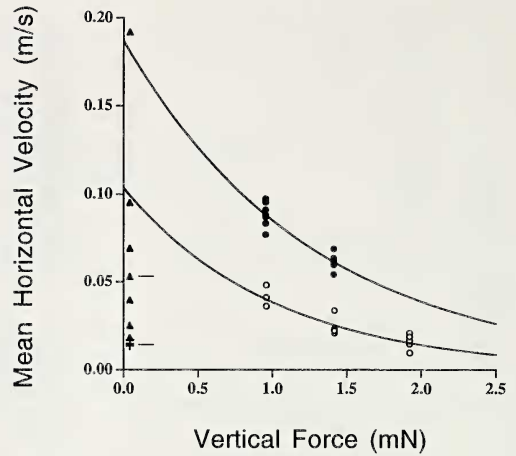

Figure 6.—During wind tunnel measurements of the horizontal terminal velocities (V_t) of sailing spiders, V_t varied with spider size as well as with mass and posture. For the large spiders (wet weight = 1.82 and 2.38 mN), the elevated posture (●) resulted in a doubling of V_t relative to V_t for the prone posture (○) (dry weight = 0.96 mN – elevated: 0.088 ± 0.007 m/sec vs. prone: 0.042 ± 0.006 m/sec, ratio = 2.12; dry weight = 1.42 mN – elevated: 0.062 ± 0.004 m/sec vs. prone: 0.024 ± 0.005 m/sec, ratio = 2.51). For the small spider (wet weight = 0.013 g), the elevated posture (▲) resulted in a 3.7-fold increase in V_t (based on comparison of medians, designated with dashes) relative to V_t for the prone posture (+). See text for statistical analyses. Exponential curves (because V_t must approach zero as vertical force becomes very large) fitted to the data for the large spiders were $0.187 \, F_v^{-0.342}$ (elevated, $r^2 = 0.873$) and $0.104 \, F_v^{-0.433}$ (prone, $r^2 = 0.766$) where F_v is the vertical force. The velocities shown here, for all but the heaviest prone spider, overestimate V_t achievable during sailing by live spiders because the dried spiders were lighter and therefore created shallower dimples and less water-generated drag (Suter 1997).

motion resembles ballooning in which, once airborne, the spider has no control over its horizontal direction and therefore little control over its destination, and in which posture is crucial (Suter 1992).

Two other parallels between sailing and ballooning are worth noting: neither requires substantial muscular input, and in both forms of locomotion, smaller individuals have substantial advantages. The energetic cost of whole-body sailing (cf. Deshefy 1981) can be estimated as the work needed for the spider to raise its body to an effective sailing height—for the larger spiders used as models in this
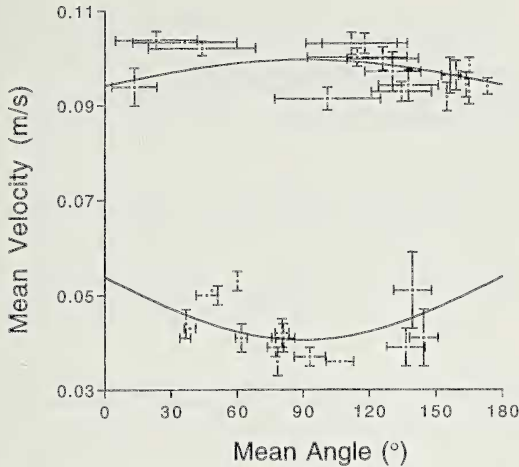
Figure 7.—Sinusoidal curve fits on the velocities of large spiders in elevated (upper) and prone (lower) postures, after release at different horizontal orientations relative to the direction of air motion in the wind tunnel, revealed that orientation had no significant effect on V_t. Each datum consists of mean $\pm$ SD velocities and angles (relative to $0°$, facing directly upwind) for one spider's motion following a single release: variation in V_t reflects measured changes in velocity between digitized frames from videotaped records; variation in angle is a consequence of the slow rotation of the released spider during its movement downwind. For the elevated posture, $V_t = 0.005$ sin (angle) $+ 0.094$ ($r^2 = 0.119$, $n = 19$, $P > 0.05$), and for the prone posture, $V_t = 0.013$ sin (angle) $+ 0.054$ ($r^2 = 0.144$, $n = 17$, $P > 0.05$).

study (live weight $\sim$ 2.1 mN), the work required to raise the center of mass from 4–12 mm above the water is about 1.68×10^{-5} joules, an amount of work that needs to be done only once during a sailing episode. In comparison, for the smaller of the spiders used as models in this study (live weight = 0.126 mN), the cost of elevating the center of mass 2.3 mm is about 2.90×10^{-7} joules. The smaller spider's velocity in the elevated posture is approximately the same as that of the larger spider (Fig. 6), but the cost of attaining that posture for the larger spider is 58 times as great. Thus, the efficiency of sailing is far greater for very small spiders, but for any spider the cost is very small: consumption of a single fruit fly (Golley 1961) would provide sufficient energy to elevate the larger spider thousands of times! Sailing is, like ballooning (Suter 1999b), a remarkably cheap form of transport.

Risk assessment.—Fishing spiders are attacked from below by fish (G. Miller pers. commun.) and are likely also to suffer predation from above by anurans and birds. Because their predators' feature detectors undoubtedly respond to specific cues (e.g., shape, size, motion: Lettvin et al. 1959; Ewert 1974; Ewert et al. 1983) the suppression of any of these cues can result in a reduction in the probability of eliciting predation. In this context, sailing can be viewed as an inconspicuous form of locomotion that offers a relative reduction in predation risk through the suppression of visual cues: propulsive motions of the legs relative to the body are absent, and surface waves caused by rowing and galloping locomotion (Suter et al. 1997; Suter 1999a) are not generated at the velocities achieved during sailing (Fig. 6; Denny 1993; Vogel 1994).

Another kind of risk, that associated with motion whose direction is not controlled by the spider, should rise with elevated uncertainty about the ecological suitability of the destination. In the ponds usually inhabited by *D. triton*, this risk is minimal because the ultimate destination of a sailing spider will always be an edge of the pond, a location that may be unfamiliar to the spider but that is apt to be as ecologically suitable as the spider's original location. In contrast, species of *Dolomedes* that inhabit the shores of islands in the Great Lakes of North America cannot be assured of a benign destination if the wind is offshore: sailing away from a shore can take the spider into open waters where both food and cover are unavailable and where the direction of the nearest shoreline is undetectable.

Function.—For fishing spiders living at the edges of ponds, sailing is both energetically cheap and relatively safe (above). But this form of locomotion has only rarely been observed in nature and its function in the context of more controlled modes of locomotion on the water surface (Suter et al. 1997; Suter 1999a) remains unclear. Because sailing is most efficient for smaller spiders (Fig. 6) and because heavy *D. triton* are unable to elevate their bodies into rapidly moving air without exceeding the ability of the water's surface tension to support them (Suter 1999a), the primary function of sailing may be to facilitate

dispersal in young spiders, a hypothesis that is yet to be tested.

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